

# Is nestedness in mutualistic networks an evolutionary spandrel?

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Mutualistic networks have been shown to involve complex patterns of interactions among animal and plant species. The architecture of these webs seems to pervade some of their robust and fragile behaviour. Recent work indicates that there is a strong correlation between the patterning of animal-plant interactions and their phylogenetic organisation. Here we show that such pattern and other reported regularities from mutualistic webs can be properly explained by means of a very simple model of speciation and divergence. This model also predicts a co-extinction dynamics under species loss consistent with the presence of an evolutionary signal. The agreement between observed and model networks suggests that some patterns displayed by real mutualistic webs might actually represent evolutionary spandrels.

Keywords: Ecological networks, mutualism, tinkering, evolutionary spandrels, evolution

## I. INTRODUCTION

Ecological networks are well known to exhibit a number of structural features associated with their interaction patterns (1,2,3). Those include, in particular: (a) small world structure (4) where two given species are separated by a small number of links from any other species in the web (5,6,7), (b) heterogeneous distributions of connections (1,8) where the number of links between a given species and other species in the web can vary widely; (c) modular organisation (7,9) implying that subsets of species exhibit more connections among them than with the rest of the network and (d) nestedness (10), where specialists interact with a subset of the whole set of species that generalists interact with.

The presence of some of these traits has important implications for the persistence and reliability of diverse ecosystems. As an example, it was shown earlier that the architecture of ecological food webs is consistent with the "robust-but-fragile" metaphor of complex networks: these webs are robust against the removal (extinction) of a random species but the removal of certain species can lead to a cascade of extinctions due to the existing chains of species dependencies (1, 11).

Mutualistic networks describe species interactions across two adjacent trophic levels (of consumers and their resources), such as flowers and the insects that feed on and pollinate them. The bipartite graphs that these interactions form are considered the building blocks of biodiversity (12) and they are often significantly nested (13). Yet while the robustness of ecological networks might in

large part be due to the presence of such structure, what is much less clear is from where or what that structure arises.

Following an adaptationist view of naturally evolved systems, it has been argued that the presence of these properties, nestedness in particular, is a consequence of some underlying selection process that reduces competition relative to the benefits of facilitation and hence increases biodiversity and food web persistence or feasibility (3, 14, 15), although this has been challenged (16). The main arguments provided to support this view are grounded in the use of multispecies dynamical systems, based on generalised Lotka-Volterra equations with different functional responses. Several recent papers have questioned the conclusion that nestedness has resulted from selection pressures (17) favouring higher biodiversity. Instead, it has been suggested that nestedness is likely to be a consequence (instead of a causative property) of biodiversity, in particular of the heterogeneous distributions of connections.

Other studies seem to support this view, where a structural pattern is incorrectly pointed to as a causal agent for a given functional trait and the biological details of the system under consideration. In this context, previous work concerning the evolution of complex biological and artificial networks suggest that many architectural patterns displayed by these graphs are an inevitable byproduct of the way they are constructed (18). This is in fact the consequence of processes involving network growth through duplication and rewiring (19, 20, 21, 22, 23). Specifically, evolution often proceeds by tinkering from available components (24, 25) and a network (including the proteome, metabolic networks and even technological graphs) resulting from a process of copy and further modification is likely to display complex features. Simple models involving no functionality or population dynam-

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ics can develop small world or scale-free webs, which can be modular (26) despite the apparently well established idea that modularity is an evolved, functionally relevant trait. If this were the case for mutualistic webs, their invariant features (27) would be a consequence of universal properties of the graphs and their growth rules, closer to the idea of *universality* (28, 29). When this occurs, very simple, toy models are capable of accounting for the global features exhibited by the system.

The key lesson of the studies mentioned above is that, when dealing with complex biological networks, it is important to consider the generative rules responsible for their growth and change. Some of these very ubiquitous patterns might be a byproduct of these rules, although they might be relevant or even functionally important afterwards. The emergent patterns can thus be *evolutionary spandrels*, i.e., phenotypic characteristic that evolved as a side effect of a true adaptation (30,31). Despite some criticisms related to the appropriateness of the architectural analogy (32) the key concept of a non-adaptive structural patterns stands. An example of spandrel is provided by the distribution of network motifs in cellular networks (33) where it has been shown that the conserved, uneven distribution of some small subgraphs can be explained by means of non-functional models. We can define evolutionary spandrels as structures that: (i) are the byproduct of building rules; (ii) have intrinsic, well-defined, non-random features; and (iii) their structure reveals some of the underlying rules of construction (33).

Here we aim to show that nestedness, as well as other key statistical features of mutualistic webs, can be recovered as a byproduct of the generative rules associated with the creation of diversity through speciation-divergence dynamics with no consideration of the underlying population dynamics. This approach ignores the ecological time scale (and thus all factors associated to standard stability criteria) by considering instead a scenario where speciation and diversification that takes place over very long (evolutionary) time scales. Such kind of model has been used to model macroevolutionary dynamics using both adaptive dynamics on fitness landscapes as well as models of network growth and extinction (34,35,36,37,38,39,40). These class of models has been able to give insight into the large-scale evolution of ecological networks (41, 42 and references therein). A crucial point of using these models is that we can explore the outcome of evolutionary rules that drive the structural patterns of connectivity beyond the ecological time scale.

## II. SPECIATION-DIVERSIFICATION MODEL

The approach taken here makes some strong assumptions. One is that species are either present or absent, with no role to be played by population size or other species-specific traits. Secondly, interactions are intro-

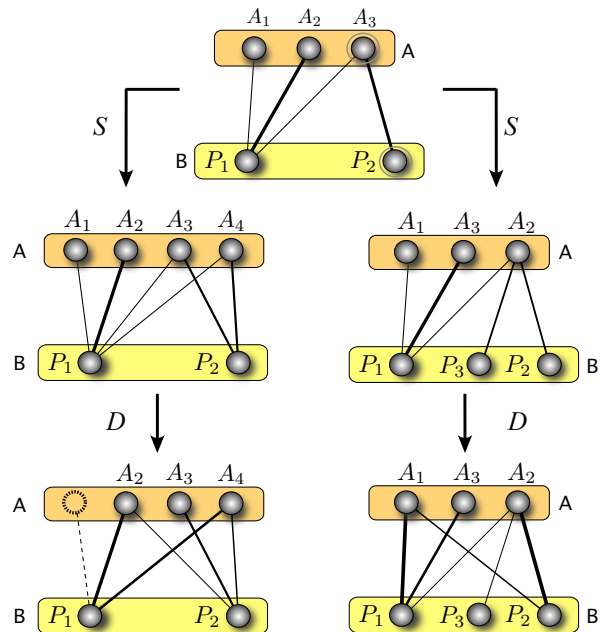


FIG. 1 Duplication-divergence rules: (a) The graph is composed of two layers involving animals (upper) and plants (lower). Speciation can affect either the  $A$  or the  $P$  sets (left and right sequences, respectively). Each time a new species is added (b) the daughter inherits all its interactions. Afterwards, they experience a divergence (c) affecting the weights and links.

duced as weighted links. The values of these links will evolve in time following very simple rules. The large-scale dynamics of our system is obtained by a combination of two processes that obviously occur over evolutionary time scales: new species are generated from old ones through speciation and coevolution and external (either environmental or stochastic) factors modify the presence and strength of the interactions.

Our model assumes a bipartite graph  $G$  involving two subsets  $A(t)$  and  $P(t)$  that correspond to the animals and plants, respectively, at a given evolutionary time step  $t$ . These species are linked (figure 1) provided that a mutualistic relationship exists. Here we consider the effect of animals on plants, weighted through a matrix  $W_{ij} = W(A_i \rightarrow P_j)$  that indicates the strength of the interaction between both partners. This can be interpreted in terms of the number of dependencies existing between the given pair (in one direction). The evolutionary dynamics are defined by a simple set of rules:

**Speciation:** we choose a given species  $A_i$  or  $P_j$  and create a speciation event. The new species inherits exactly the same list of links from its parent species. If  $A_k$  indicates the newly created species, then we have  $W_{kj} = W_{ij}$ .

**Divergence:** we redistribute the weights between parent and daughter species. A random number  $0 < \mu < 1$

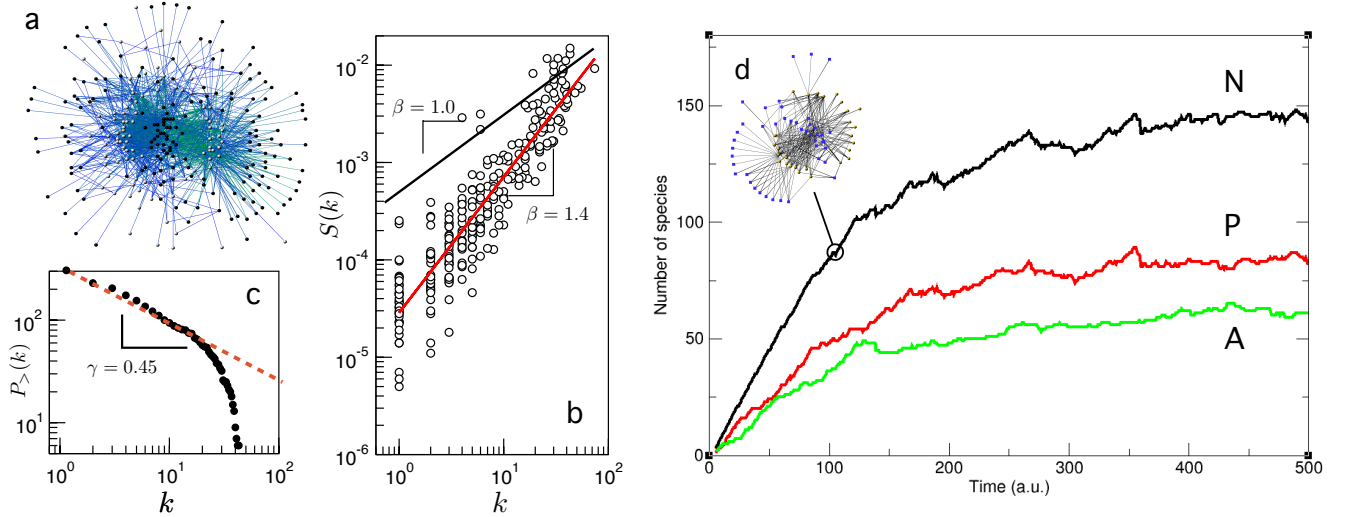


FIG. 2 (a) an example of the structured, heterogeneous network resulting from the growth dynamics with speciation and divergence (see text). Here dark and light nodes indicate "plants" and "animals". In this example,  $N = 267$  species were present at the end of the simulation, after  $T = 500$  speciation-divergence steps. The strength of the links is shown by a color scale. Greener and bluer links indicate stronger and weaker connections, respectively. In (c) the undirected degree distribution of the graph shown in (a) is displayed in a log-log plot. We can see that the system follows a broad distribution. The plot (d) shows the strength-degree correlation, which gives a power law  $S(k) \sim k^\eta$  with  $\eta = 1.4 \pm 0.05$ . The linear expectation is also shown (black line) for comparison. Here we have used  $\beta = 10^{-5}$ ,  $p = 0.1$  and  $\theta = 10^{-6}$ . An example of the time series generated by the model is shown in (d) with a snapshot of the whole graph at some intermediate time (here  $t = 100$ ).

is generated and each pair of links  $\{W_{kj}, W_{ij}\}$  is updated to a new pair  $\{\mu W_{kj}, (1 - \mu)W_{ij}\}$ . Additionally, for each link, we introduce, with a given probability  $p$ , a weight change, i. e., we have a new value

$$W_{ij} \rightarrow W_{ij} \pm \xi \quad (1)$$

with  $\xi$  being a small random number between zero and  $\beta$ . Here the parameter  $\beta$  will weight how fast evolutionary changes occur at the level of single ecological links. If  $W_{ij}$  falls below a threshold  $\theta$ , it is removed. Finally, a maximum input weight is allowed for all plants. Specifically, if the sum

$$S_j = \sum_i W(A_i \rightarrow P_j) \quad (2)$$

over all animals acting on the plant  $P_j$  is larger than one, the change is not accepted. A symmetric rule is used to constraint the links in the  $P \rightarrow A$  direction.

Because of the type of dynamics defined by the previous rules, species become extinct when no mutual support is present (i. e. if  $\sum_j W_{ji} = 0$ ). This is the simplest way of defining the mutual cooperation among species.

The model successfully generates networks with all the reported statistical patterns displayed by empirical webs. In figure 2a-b we show an example of a graph obtained from our rules, starting from an initial condition with two species at each level, connected to each other with a small weight  $W_{kl} = 10^{-3}$ . The webs are heterogeneous, showing broad scale distributions of connections (figure

2c). Specifically, if  $k_i^a$  and  $k_j^p$  indicate the number of links (or degree) of  $A_i$  and  $P_j$ , respectively, the frequency of species having a given number of links  $k$  will be indicated by  $P(k)$ . It has been found that for mutualistic webs the appropriate form of these distributions is (27):  $P(k) \sim k^{-\gamma} \exp(-k/k_c)$  where  $\gamma$  is the exponent that indicates how rapidly the distribution falls at small  $k$  and  $k_c$  a cut-off that effectively limits the spread of the distribution (43). The larger  $k_c$  the more flat is the distribution and the more common the presence of highly-connected species. In figure 2c we represent the cumulative degree distribution  $P_>(k)$  defined as:

$$P_>(k) = \int_k^\infty P(k') dk' \quad (3)$$

This distribution allows to smooth out the fluctuations and to define better estimates of the two characteristic parameters  $\gamma$  and  $k_c$ . Our model correctly predicts the broad distribution scenario, thus indicating that heterogeneity is a consequence of amplification-divergence phenomena, consistently with previous studies (19) but in this case applied to a bipartite system.

Another property of the network that can be easily determined is the aggregated *strength* of the nodes, defined as the sum of all the dependencies in both directions i. e.

$$S_i = \sum_{j=1}^{N_i} (W_{ij} + W_{ji}) \quad (4)$$

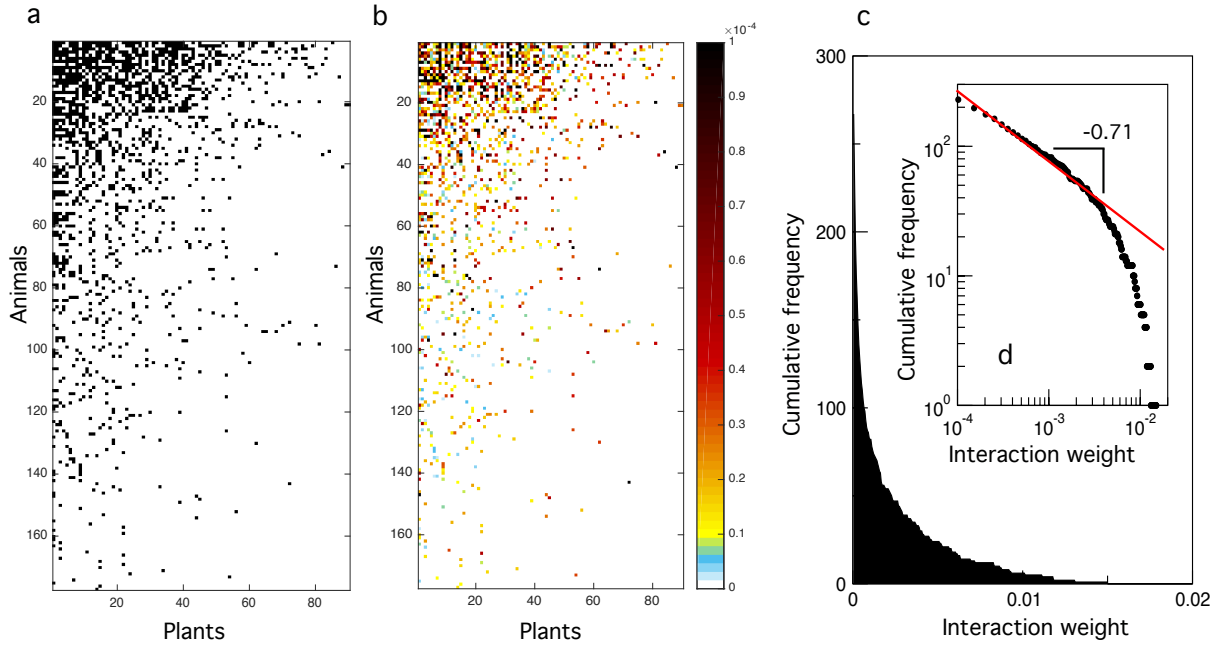


FIG. 3 The matrix of interactions between the two layers of our bipartite graph model of mutualistic interactions. In (a) we display the adjacency matrix, where black points indicate the presence of a connection. Arrows and columns have been Figure (b) show the weights of these links. In (c) the distribution of link weights is displayed, again exhibiting a truncated power law, i. e.  $P(s) \sim s^{-\gamma_s} \exp(-s/s_c)$ .

Where  $N_i$  indicates the number of interactions with other species. The use of a weighted network provides relevant information about its local and global organisation (44,45,46) and was early identified as an essential feature of mutualistic interactions (47). In general, a scaling law relates strength and degree, namely

$$S(k) \sim k^\eta \quad (5)$$

where the exponent  $\eta$  will establish the nature of the correlation. For a randomly distributed set of weights, it can be shown that a linear relation ( $\eta = 1$ ) exists. However, if the importance of a given node in the network is lower than predicted by its degree, then we would observe  $\eta < 1$ . In mutualistic webs, it has been shown that a superlinear behaviour is found, i. e.  $\eta > 1$ , indicating that species with many connections tend to display stronger interactions than the average. This is the case of real webs and also occurs in our model, as displayed in figure 2d. In our simulated system, we have  $\eta = 1.40 \pm 0.05$  which is also close to measured data (45).

The previous patterns of network organisation reveal that some key statistical regularities found in mutualistic webs can be obtained from our minimalistic assumptions. These results are the first indication that the large-scale organisation of mutualistic webs could be a side effect of the amplification dynamics associated to the copy-and-divergence dynamics associated to the rules considered here. What about nestedness? Is this property also an emergent phenomenon resulting from evolutionary dy-

namics, decoupled from the underlying ecological dynamics?

### III. NESTEDNESS FOR FREE

In this section, we study the nestedness property associated our model. We show that our model exhibits nestedness without any additional stability requirement. A quantitative (weighted) approach to nestedness (unlike binary measures) takes into account species abundances and interaction frequencies.

A bipartite network  $G = (A, P, E)$  has two disjoint sets of nodes  $A$  and  $P$  representing animals and plants, respectively. Let  $N_A = |A|$  be the number of animal species and  $N_P = |P|$  be the number of plant species, i.e., the total number of species in our system is  $N = N_A + N_P$ . Now, assume that animals are indexed  $1, 2, \dots, N_A$  and plants are labeled  $N_A + 1, N_A + 2, \dots, N_A + N_P$ . The matrix of mutualistic interactions  $W = [W_{ij}]$  has a block off-diagonal form like this:

$$W = \begin{bmatrix} 0 & W_{N_A \times N_P} \\ W_{N_P \times N_A} & 0 \end{bmatrix} \quad (6)$$

where 0 is the all-zero matrix that reflects the bipartite constraint, i.e., there are no interactions between any pair of alike species. The so-called *bipartiteness* function  $\nu(u)$  indicates  $u$  node type, e.g., where the vertex belongs

to one type ( $\nu(u) = 0$ ) or the other type ( $\nu(u) = 1$ ). Using this notation, bipartite edges  $(u, v) \in E$  must satisfy  $\nu(u) + \nu(v) = 1$ .

Edges in a nested network are organised in a way that specialists interact with subset of the species whom generalists interact with. This nested pattern can be detected in the specific arrangement of present and absent interactions in bipartite networks. Recently, this nestedness definition was extended to quantitative networks using spectral graph theory.

It can be shown that the largest eigenvalue of bipartite networks determines nestedness (16). This is a robust measurement of nestedness because its invariance to the sorting of rows and columns in the matrix. First, we define the  $N_A \times N_P$  incidence matrix  $B = [B_{ij}]$ :

$$B_{ij} = \frac{1}{2}(W_{i,j+N_A} + W_{j+N_A,i}) \quad (7)$$

where  $1 \leq i \leq N_A$  and  $1 \leq j \leq N_P$ . We can interpret this bipartite matrix as the average interaction frequency between a pair of (animal, plant) after discarding link direction. Because  $B$  is a symmetric matrix, all its eigenvalues are real and distributed symmetrically around 0. The spectral radius  $\rho(B)$  (or dominant eigenvalue) is the largest eigenvalue associated to the matrix  $B$  and it represents a natural measurement of nestedness: large values of  $\rho(B)$  correspond to highly nested matrices.

Nestedness is a relative value that depends on the size (number of species  $N$ ) and fill (density of interactions) of the bipartite matrix  $B$ . In order to assess its relevance, we compare the observed value of nestedness in the model with an ensemble of random matrices with similar properties (48, 49). Here, we use the null model proposed by (16), which keeps the structural features of the network while swapping the order of weighted links (so-called 'binary shuffle' in (49)). We assess the significance of empirical nestedness with the Z-score:

$$Z = \frac{\rho(B) - \langle \rho \rangle}{\sigma_\rho} \quad (8)$$

where  $\langle \rho \rangle$  and  $\sigma_\rho$  are the average value and the standard deviation of the network measure in a random ensemble, respectively. Here, we consider that mutualistic networks are significantly nested whenever the corresponding  $Z > 2$  (i.e.,  $p < 0.05$  using the Z-test).

What is the impact of parametric changes on the statistical properties of these webs? A systematic exploration reveals that the previous conclusions are robust. The main parameter associated to our model is  $\beta$ , which provides a measure of the allowed speed of network changes through evolutionary time. We have explored the impact of this parameter on the connectance, mean network strength and spectral radius and nested organisation of these webs (see figure 4). Our model predicts highly significant nestedness for a wide range of parameters, i.e., when  $\beta < 0.001$ . On the other hand, the grey

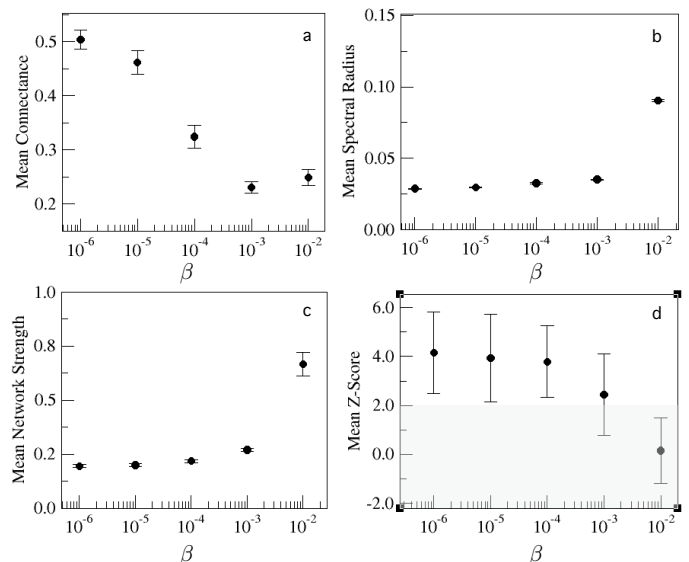


FIG. 4 The effect of the maximum link change  $\beta$  on the structural patterns exhibited by mutualistic model networks: (a) mean connectance decays with faster evolutionary rates, (b) nestedness is stable for wide range of parameters and (c) it correlates with network strength, (d) statistical significance of the nestedness drops for high evolutionary rate, i.e.,  $\beta > 0.01$ . Here we have used link probability  $p \in [0, 1]$  and tuned  $\beta$  over several orders of magnitude. Overall, these plots comprise 600 random samples taken uniformly from the phase space  $(p, \beta)$ .

region in Figure 4d corresponds to distributions of spectral radius scores in an ensemble of random matrices. The results described here support the hypothesis that and evolutionary-scale, minimal model generates highly nested bipartite networks in a wide range of scenarios.

#### IV. DISCUSSION

In this paper we have introduced a very simple model of large scale evolution of mutualistic webs. It includes the most elemental requirements associated to the measurable web properties. It ignores all details except minimal components related to the creation of new species through speciation and the change (under constraints) of weights over evolutionary time. Despite its simplicity, the model is capable of consistently reproducing several well known structural patterns of organisation, suggesting that the generative rules responsible for network growth largely determine the presence of universal traits in empirical systems. The model incorporates a restriction to the total amount of inputs received and the persistence of species is guaranteed provided that a link exists between this species and at least one mutualistic partner.

Generative models of network structure are seldom rare mutualistic networks in comparison with other ecological networks, e.g. antagonistic ones. The model presented here is not the only one trying to explain the emer-

gence of complex mutualistic networks. In (50) the authors showed that nestedness and heterogeneous degree distributions emerge from an optimization principle that maximizes species abundances. Their model, however, works over ecological time-scales, while the question we asked here is to what extent simple evolutionary models can account for observed structural patterns. In this respect, Nuismer et al (2013) developed a quantitative genetic model that allows inference of network structure over evolutionary time. Their model was far more complex than the one presented here, but they only found that emerging networks were more nested than their random counterparts under very restrictive conditions: species interactions should be mediated by phenotype differences and coevolutionary selection should be weak. In the remaining cases, resulting networks were either not nested or anti-nested.

Duplication-rewiring models are known to indirectly incorporate a preferential attachment rule. This rule is known to generate heterogeneous, sometimes long-tailed degree distributions (51). Once heterogeneous distributions arise, other features can come "for free": nestedness in particular has been shown to be largely a consequence of broad connectivities (52, 53).

Our model incorporates evolutionary rules of speciation and drift that naturally provide a mechanism to explain the properties found in mutualistic webs. Since our model does not include the population size associated to each species nor the nonlinear dynamics of ecological interactions, our results suggest that there is no need to assume that the ecological scale plays a major role in shaping mutualistic webs. Instead, the universal constraints associated to the evolutionary unfolding of these webs would lead to the observed invariant properties.

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